

LINKAGE STUDIES IN *PHARBITIS NIL*. I.

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Received January 6, 1930

TABLE OF CONTENTS

	PAGE
INTRODUCTION	26
Variegated linkage group	26
Cordate linkage group	28
Yellow linkage group	30
Acuminate linkage group	32
Contracted linkage group	32
Speckled linkage group	35
Delicate linkage group	35
Pear linkage group	35
Duplicated linkage group	36
Retracted linkage group	37
Miscellaneous	38
CONCLUSION	39
SUMMARY	40
LITERATURE CITED	41

INTRODUCTION

In *Pharbitis Nil*, the Japanese morning glory, 10 linkage groups have been detected, including 34 genes (IMAI 1929). Further studies show that the rayed linkage group is absorbed into the contracted group and a new retracted group is established. Therefore, we have still 10 linkage groups in this plant, but containing 50 loci instead of the previous 34. In this paper the writer attempts to present only new linkage data which do not overlap those given in the previous report. For a description of the characters the reader is referred to the writer's register note (IMAI in press). To save space various tables showing independent segregation are omitted.

VARIEGATED LINKAGE GROUP

Four genes, variegated (v), crumpled-1 (c_1), Blown-1 (B_1) and fasciated-3 (f_3), were found to be included in the variegated linkage group. The recombination percent was 17.7 for v and c_1 , 29.3 for v and B_1 , and roughly 20-25 for v and f_3 . Further experiments bring in 4 genes which are found to be grouped with them. On selfing F_1 obtained by crossing variegated with brown (b_r), the writer recorded F_2 as shown in table 1.

The data show linkage between variegated and brown; therefore brown is considered to be included in this linkage group. This fact is still further

TABLE 1
F₂ from the cross of variegated by brown.

CROSS	+	v	b _r	v b _r	TOTAL
401×405	45	19	11	0	75
402×405	46	17	23	0	86
Total	91	36	34	0	161

substantiated by the additional linkage data between crumpled-1 and brown. From crosses between crumpled-1 and brown, the writer obtained F₂ as indicated in table 2.

TABLE 2
F₂ from the cross of crumpled-1 by brown.

CROSS	+	c ₁	b _r	c ₁ b _r	TOTAL
401×405	48	16	11	0	75
402×405	40	23	23	0	86
Total	88	39	34	0	161

Feathered is a character recessive to normal, and even (*e_v*) acts as a modifier for feathered. A cross was made between 2 "parental stocks"; 1, variegated and heterozygous for feathered, the other, heterozygous for deformed (*d_e*). Among a number of F₂ families, 3 gave practically the same results, showing segregation for variegated, feathered, even and deformed, as shown collectively in table 3.

TABLE 3
F₂ showing linkage between variegated and even.

CROSS	+	v	f _e	f _e v	e _v	e _v v	d _e	d _e v	TOTAL
189s×215s	180	58	42	12	15	0	45	10	263

Of the segregating genes, feathered was known to be included in the cordate linkage group, and deformed is found to be linked with yellow, which constitutes, together with the other genes, the yellow linkage group. Therefore the 3 genes, variegated, feathered and deformed, segregate independently of each other in simultaneous assortment. Even acts as a modifying character to feathered. The segregating ratio is expected to be 36 normal (27+++; 9+e_v+) : 9 feathered (9f_e++) : 3 even (3f_ee_v+) : 16 deformed (9++d_e; 3f_e+d_e; 3+e_vd_e; 1f_ee_vd_e). The deficit of deformed in table 3 is due to its low viability. Among a total of 362, 15 were even and none of them were variegated. This shows linkage be-

tween variegated and even. Therefore, the variegated linkage group is increased by 1 more gene, namely, even.

Faded (f_d) may be included as an additional member to this group from the data in table 4, which is an F_2 obtained by crossing variegated faded with normal.

TABLE 4
F₂ from the cross of variegated faded by normal.

CROSS	+	v	f_d	v f_d	TOTAL	w_2
410×415	47	8	11	9	75	(28)
N×VF	75	15	13	11	114	..
26×CT	65	13	12	11	101	..
Total	187	36	36	31	290	..

The recombination frequency is calculated as 31.0 percent. The relation of faded to the other members of this linkage group is not yet known, so we cannot decide the locus in the linear arrangement.

In addition to the above data, the writer obtained another dependent segregation for variegated and couple (c_u), as indicated in table 5.

TABLE 5
F₂ from the cross of variegated by couple.

CROSS	+	v	c_u	v c_u	TOTAL
420×34	180	68	67	10	325

The frequency of recombination for variegated and couple is 37.7 percent. In F_2 of the other cross of crumpled-1 (No. 420) and couple (No. 425), the writer obtained data for crumpled-1 and couple, giving a practically free segregation of 202 normal, 60 crumpled-1, 61 couple and 22 crumpled-1 couple among a total of 345. This fact shows that variegated is present between crumpled-1 and couple.

CORDATE LINKAGE GROUP

This group was known to include 3 genes, cordate (c_o), feathered (f_e) and semi-contracted (s_e). The percentage of recombination was 1.2 for c_o and f_e , 18.6 for s_e and c_o , and 17.7 for f_e and s_e . Therefore, the linear arrangement of these genes on the cordate chromosome is probably $c_o-f_e-s_e$, with a distance of 1.2 between c_o and f_e , and 17.7 between f_e and s_e . Further data furnish 3 additional genes as members of this group. In F_2 , obtained by crossing cordate with precocious (p_e), the writer recorded the linkage data presented in table 6.

TABLE 6
F₂ from the cross of cordate by precocious.

CROSS	+	<i>c_o</i>	<i>p_c</i>	<i>c_o p_c</i>	TOTAL
410×190	179	79	84	5	347

The frequency of recombination is 24.6 percent. The relation of *p_c* to *s_c* being not yet determined, we cannot decide whether *p_c* is located at the left of *c_o* or at the right of *s_c*. Two genes, crêpe (*c_p*) and palmate (*p_l*), are found to be linked with each other, and also with precocious. In table 7 the *F₂* data show repulsion for *p_c* and *p_l*.

TABLE 7
F₂ from the cross of precocious by palmate.

CROSS	+	<i>p_c</i>	<i>p_l</i>	<i>p_c p_l</i>	TOTAL
297×929	105	45	46	5	201

The recombination percent is 31.3. The linkage of palmate with crêpe, is shown by the data in table 8.

TABLE 8
F₂ from the cross of palmate crêpe by normal.

CROSS	+	<i>p_l</i>	<i>c_p</i>	<i>p_l c_p</i>	TOTAL
297×929	123	30	27	21	201

The recombination frequency due to crossing over is estimated to be 34.6 percent. With the proofs that *p_c* is linked with *p_l* and that *p_l* is linked with *c_p*, we expect a dependent relation between *p_c* and *c_p*. Actually the segregation shows linkage between them, as can be seen by inspecting the data in table 9.

TABLE 9
F₂ from the cross of precocious by crêpe.

CROSS	+	<i>p_c</i>	<i>c_p</i>	<i>p_c c_p</i>	TOTAL
297×929	110	43	41	7	201

The frequency of recombination is 38.8 percent. With the recombination percent of 31.3 for *p_c* and *p_l*, 34.6 for *p_l* and *c_p*, and 38.8 for *p_c* and *c_p*, the arrangement of the 3 genes in cordate chromosome is probably *p_c—p_l—c_p*, but we cannot decide definitely without further proof. Cordate shows sometimes a very weak linkage with *c_p* (IMAI 1924) and, sometimes, practically independent segregation. Among the 3 genes above presented,

p_c , therefore, may be located nearest to c_o . Owing to insufficient information on relation of these 3 linked genes, precocious, palmate and crêpe, to the other previously known linked genes, cordate, feathered and semi-contracted, we cannot arrange their loci beyond the facts described above and in the previous paper.

The proof of independent segregation of the genes included in the cordate linkage group in relation to those included in the variegated group is as follows. Cordate to v , c_1 and B_1 ; f_e to v and B_1 ; s_e to v and c_1 ; p_e to c_1 ; $c_p r$ (reversed, allelomorphic to c_p) to v , c_1 and B_1 .

YELLOW LINKAGE GROUP

The yellow linkage group was noted as including 2 genes, yellow (y) and dusky (d_y), the recombination frequency being 1.0 percent. The later experiments add 3 genes, light (l_t), deformed (d_e) and speckled-reduced ($s_p r$), to this group. Light dilutes the flower color, acting on intense. In F_2 from the cross of light with dusky the writer obtained the data showing linked segregation for dusky and light, as shown in table 10.

TABLE 10
F₂ from the cross of dusky by light.

CROSS	+	d_y	l_t	$d_y l_t$	TOTAL
421×430	93	45	32	0	170
422×435	94	45	34	0	173
Total	187	90	66	0	343

The same crosses were also segregated for yellow or yellow-inconstant (y^i), the latter being recessive to normal but dominant to yellow, and constituting triple allelomorphs with normal and yellow (IMAI 1930b). The relation between yellow and dusky in these crosses shows close linkage as expected and will not be cited here. In table 11 are shown the F_2 data for light and yellow or yellow-inconstant.

TABLE 11
a. F₂ from the cross of yellow by yellow-inconstant light.

CROSS	y^i	y	$y^i l_t$	$y l_t$	TOTAL
421×430	93	55	31	1	170

b. F₂ from the cross of yellow-inconstant by light.

CROSS	+	y^i	l_t	$y^i l_t$	TOTAL
422×435	94	45	34	0	173

The data indicate considerable closeness of the 2 loci yellow and light. Owing to repulsion in these crosses and the data not being sufficient, the calculation of the recombination frequency is not of much importance, since it does not give a reliable figure. Now it is quite evident that the light locus is situated rather near to those of dusky and yellow.

TABLE 12

Some of F₂ from the cross of yellow by normal heterozygous for deformed.

FAMILY NO.	+	y	d _c	y d _c	TOTAL
1	225	101	71	2	399
5	23	10	5	1	39
6	91	52	29	0	172
8	92	54	23	0	169
Total	431	217	128	3	779

The linkage data for deformed were furnished by the other F₂ (table 12).

Owing to the low viability of deformed there was a deficiency of its segregates. The deformed plants were 128 not-yellow and 3 yellow, on the basis of which figures the recombination frequency is about 15 per cent. The writer also obtained coupling data proving linkage between yellow and deformed, but the data were meagre in number and will not be cited.

Speckled-reduced is a modifying gene for speckled and is linked with yellow. The data furnishing linkage between yellow and speckled-reduced are shown in table 13.

TABLE 13

F₂ from the cross of yellow (speckled) by speckled-reduced (speckled).

CROSS	+	y	s _p -r	y s _p -r	TOTAL
410×440	52	28	26	1	107
410×445	72	23	31	4	130
Total	124	51	57	5	237

The percent of recombination is 28.5. This indicates that speckled-reduced is located farther from yellow than deformed is. The relation of speckled-reduced to the other genes of this linkage group is not yet known.

The independent relations of the genes of the yellow group to those of the variegated and cordate groups are as follows: For the former, y or yⁱ to v, c₁, B₁, f_d and c_u; d_y to v, c₁, B₁, f_d and c_u; l_t to v and c_u; s_p-r to c₁. For the latter (the cordate group), y or yⁱ to c_o, f_e, s_c and c_p; d_y to c_o, s_c and c_p; l_t to s_c and c_p; s_p-r to c_o, p_c and c_p.

ACUMINATE LINKAGE GROUP

Three genes, acuminate (a_c), Margined-2 (M_{r2}) and magenta (m_g), were known for the acuminate linkage group. The percentage of recombination was about 0.5 for a_c and M_{r2} , and 21.2 for a_c and m_g . No linked genes have been detected to add new data. The independent relation in segregation is observed in the following cases. For the variegated linkage group, a_c to B_1 , f_d and c_u ; m_g to v , c_1 , B_1 , f_d^s (smeary, allelomorph to f_d) and c_u . For the cordate group, a_c to c_o , s_c and c_p ; m_g to c_o , s_c and c_p (c_p^r). For the yellow group, a_c to y (y^i) and d_y ; m_g to y and d_y .

CONTRACTED LINKAGE GROUP

From the results of the former experiments the writer reached the conclusion that the contracted linkage group contains 8 genes, interaxil-green, contracted, Margined-1, tube-white, intense, Margined-reduced, white-2 and dragonfly. It was, however, an error to put the 2 genes, white-2 and dragonfly, in this group. The gene for the intensity of the flower color, being linked with white-2, is not intense as previously described, but Dilute. So the two genes, white-2 and dragonfly, must be joined to the duplicated linkage group and excluded from the contracted group. HAGIWARA (1922) considered that dragonfly is weakly linked with contracted and Margined-1, but according to the writer's new data the relations are quite independent. In the previous paper, the writer arranged the genes, excluding w_2 and d_g , in the following order in the chromosome: i_g — c_t — M_{r1} — t_w — i , putting the locus of i_g at 0, of c_t at 5.5, of M_{r1} at 6.5, of t_w at 13.6, of i at 38.2, and of M_{r-r} at 38.2 ± 3.0 .

The later experiments show that the group formerly called rayed is to be combined with this group, and 3 new genes are also included therein. In all, the contracted linkage group contains 11 genes which are interaxil-green (i_g), contracted (c_t), Margined-1 (M_{r1}), tube-white (t_w), intense (i), Margined-reduced (M_{r-r}), Rayed (R_y), cream (c_r), shrubby (s_h), duskish (d_h) and purple (p_r).

In F_2 of crossing interaxil-green by Rayed the data show linkage between interaxil-green and Rayed, as indicated in table 14.

TABLE 14
F₂ from the cross of interaxil-green by Rayed.

CROSS	R_y	+	$i_g R_y$	i_g	TOTAL	w_1
470×450	75	6	4	25	110	(34)
471×450	32	5	1	8	46	(21)
Total	107	11	5	33	156	(55)

The percentage of recombination is 10.3. Tube-white was known to be located at a distance of 13.6 units from i_g . If R_y is located to the right of i_g there must be very close linkage between t_w and R_y . Actually, however, this was not the case, but weakly dependent segregation was recorded, as is shown by the data in table 15.

TABLE 15
F₂ from the cross of tube-white by Rayed.

CROSS	R_y	+	$t_w R_y$	t_w	TOTAL
475×450	150	41	40	19	250

The frequency of recombination for tube-white and Rayed is 42.5 percent. This shows that the locus of Rayed is situated to the left of i_g at a distance of about 10.3 units, and yet the figure thus obtained by adding 10.3 to 13.6 differs greatly from 42.5. As formerly stated, cream is linked closely with R_y , the recombination frequency being about 1.2 percent. Therefore cream is located either to the left or to the right at about 1.2 units distance from R_y , which is situated at roughly 10.3 units to the left of i_g .

Shrubby is a mutant character newly found (IMAI in press). The shrubby mutants occurred in one of the F_2 families obtained from a cross, and the data showed linked segregation of shrubby with interaxil-green

TABLE 16
F₂ showing linkage between interaxil-green and shrubby.

CROSS	+	i_g	s_h	$i_g s_h$	TOTAL
471×450	51	5	0	14	67

and Rayed. In table 16 is shown the relation between interaxil-green and shrubby.

The recombination percent is 3.1. The numerical relation in segregation of Rayed and shrubby is shown in table 17.

TABLE 17
F₂ showing linkage between Rayed and shrubby.

CROSS	R_y	+	$R_y s_h$	s_h	TOTAL	w_1
471×450	32	4	1	9	46	(21)

The calculation shows that the recombination percentage for Rayed and shrubby is about 11.0. These data indicate that the s_h locus is situated either to the right or to the left of i_g at about 3.1 units. Beyond this we

cannot fix the locus of shrubby on the contracted chromosome, because the data on which the calculations were made are not sufficient. With these data together we may construct a preliminary chromosome map in the relations as follows: $R_y(0)$, $c_r(\pm 1.2)$, $i_q(10.3)$, $s_h(10.3 \pm 3.1)$, $ct(15.8)$, $M_{r1}(16.8)$, $tw(23.9)$, $i(48.5)$, $M_{r-r}(48.5 \pm 3.0)$.

Duskish is also found to be included in this group. Table 18 shows the data indicating linkage between shrubby and duskish.

TABLE 18
F₂ showing linkage between shrubby and duskish.

CROSS	+	s_h	d_k	$s_h d_k$	TOTAL	w_1
471×450	28	10	8	0	46	(21)

Although the number observed is very small, it may indicate linkage between the two characters. Duskish gives linkage to tube-white, as indicated in table 19.

TABLE 19
F₂ from the cross of tube-white by duskish.

CROSS	+	t_w	d_k	$t_w d_k$	TOTAL
475×450	135	52	56	7	250

The recombination percent is 34.9. The segregation of intense and duskish also shows weak linkage, as is indicated in table 20.

TABLE 20
F₂ from the cross of intense duskish by normal.

CROSS	+	i	d_k	$i d_k$	TOTAL	w_1
470×426	72	14	12	10	108	(41)

The recombination frequency is 32.0 percent. The other data, however, show practically independent segregation of duskish to interaxil-green and Rayed. Considering all these data together we presume that the d_k locus is probably situated in the right part of the chromosome.

Purple is another gene which may be included in this group. The data show that the purple locus is probably in the right part of the chromosome, because of linkage with tube-white and duskish, but of practically independent segregation to Rayed and contracted. The data showing linkage, however, being complicated by the simultaneous segregation of other genes, will not be cited.

The proofs for the independency in segregation of the genes of this group in their relations to those of the other groups have been obtained

in the following cases: For the variegated group, i_g to c_1 ; c_t (c_t^s , star; allelomorph to c_t) to v , c_1 , B_1 and f_d ; Mr_1 to v and c_1 ; t_w to v ; i to v , c_1 and B_1 ; m_r-r^s (margined-slight, allelomorph to M_r-r) to v ; d_k to v and c_1 ; p_r to v , c_1 and c_u ; R_y to f_d . For the cordate group, i_g to c_o , p_c , p_l and c_p ; c_t (c_t^s) to c_o , f_c , s_c , p_c and c_p ; Mr_1 to c_o and s_c ; t_w to c_o and c_p^r ; i to c_o and c_p (c_p^r); m_r-r^s to c_o ; d_k to c_o , s_c and c_p ; p_r to s_c and c_p . For the yellow group, i_g to y ; c_t (c_t^s) to y , d_k and s_p-r ; Mr_1 to y^i and d_y ; i to y and d_y ; d_k to y and d_y ; p_r to y (y^i), d_y and l_i ; R_y to y . For the acuminate group, i_g to m_g ; c_t to a_c and m_g ; Mr_1 to m_g and Mr_2 ; t_w to m_g ; i to m_g ; d_k to a_c and m_g ; p_r to a_c and m_g ; R_y to a_c .

SPECKLED LINKAGE GROUP

The speckled linkage group was known to include 3 genes, speckled (s_p), white-1 (w_1) and Margined-fluctuated (M_r-f). The former 2, s_p and w_1 , are linked very closely with about 0.8 percent of recombination, and w_1 is linked with M_r-f , giving a recombination frequency of roughly 20 percent. No new genes have been detected for this group.

For the proofs of independency of the genes of this group in relation to those of the other groups the writer obtained the following cases: For the variegated group, s_p to v , c_1 and f_d (f_d^s); w_1 to v and c_1 . For the cordate group, s_p to c_o , p_c and c_p ; w_1 to s_c and c_p^r . For the yellow group, s_p to y and s_p-r ; w_1 to y . For the acuminate group, w_1 to m_g . For the contracted group, s_p to i_g , c_t , Mr_1 , d_k and R_y ; w_1 to i_g , c_t , Mr_1 , i , d_k , p_r and R_y .

DELICATE LINKAGE GROUP

For the delicate linkage group two genes, delicate (d_l) and crumpled-2 (c_2), were known, and no new genes which belong to this group have been detected since. The recombination frequency for delicate and crumpled-2 is roughly 5 percent.

The proofs for the independent segregation of delicate to the genes of the other linkage groups previously mentioned are as follows: To v and B_1 of the variegated group; c_o and c_p^r of the cordate group; y of the yellow group; a_c and m_g of the acuminate group; t_w , i , d_k , p_r , m_r-r^s and R_y of the contracted group. No data have been obtained for the relation to the genes of the speckled group. Crumpled-2 being linked very closely with d_l , the genes above cited may be independent in segregation, but no accurate data on these relations have been obtained as yet.

PEAR LINKAGE GROUP

The pear linkage group was found to contain four genes, pear (p), fasciated-1 (f_1), fasciated-2 (f_2) and Blown-2 (B_2). The recombination

frequency is roughly 20–25 percent for f_1 and f_2 , about 2.5 percent for p and f_1 , and 23.5 percent for p and B_2 . No new genes have been discovered for this group.

The writer has at hand proofs of the independence of the gene p , in its relations to the genes of the various groups, as follows: For the variegated group, to v , c_1 and B_1 ; for the cordate group, to c_o and c_p (c_p^r); for the yellow group, to y ; for the acuminate group, to a_c and m_o ; for the contracted group, to c_t , l_w , i , m_r-r^s , d_k and R_v ; for the speckled group, to s_p and w_1 ; for the delicate group, to d_l .

DUPLICATED LINKAGE GROUP

The duplicated linkage group was known to include three genes, duplicated (d_p), striped (s_t) and Dilute (D). The recombination percent is 13.7 for d_p and s_t , 25.6 for d_p and D , and 10.1 for s_t and D . Therefore, the order in the chromosome is d_p-s_t-D , with an interval of 13.7 between d_p and s_t , and 10.1 between s_t and D . As was stated in a former section, the two genes, white-2 (w_2) and dragonfly (d_o), should be really included in this group. According to the writer's calculation on the basis of MIYAZAWA's data the recombination frequency for D and w_2 is less than 1.4 percent (IMAI 1921). The writer also obtained the data showing repulsion of high degree between the two genes as shown in table 21.

TABLE 21
F₂ showing repulsion between Dilute and white-2.

CROSS	D	+	t_g	w_2	TOTAL	w_3
455×480	52	21	29	37	139	..
460×481	38	21	16	23	98	(26)
Total	90	42	45	60	237	..

The results are very close to 6 Dilute: 3 normal: 3 tinged: 4 white-2, which ratio is calculated on the assumption of complete repulsion between Dilute and white-2.

The recombination percentage for w_1 and d_o was estimated to be 25.7 on the basis of HAGIWARA's data (IMAI 1929). As is stated elsewhere (IMAI 1930a), the writer observed great deficit of dragonfly segregating in the hybrid progeny, and it prevented him from fixing the recombination frequency for white-2 and dragonfly in his own data. Quite recently, however, he bred two F_2 families, in which occurred no deficit of dragonfly, with simultaneous segregation of white-2, as shown by the data in table 22.

TABLE 22
F₂ from the cross of white-2 dragonfly by normal.

CROSS	+	w_2	d_p	$w_2 d_p$	TOTAL
420×34	207	36	33	49	325
N×WK	320	50	51	74	495
Total	527	86	84	123	820

The recombination frequency is 23.3 percent. According to fragmental data dragonfly is segregated almost independently in relation to duplicated. The order of the genes above cited on the chromosome may be $d_p-s_i-D \pm w_2-d_o$, with an interval of 13.7 between d_p and s_i , 10.1 between s_i and D , and 23.3 between w_2 and d_o .

Extended (*e*) is found to be linked with dragonfly, as shown by the data in table 23.

TABLE 23
F₂ from the cross of dragonfly by extended.

CROSS	+	d_p	<i>e</i>	$d_p e$	TOTAL
427×465	108	49	44	9	210

The recombination percentage is 38.3. The relation of extended to the other members of this group, however, is not yet known.

The data in regard to the independence of relations have been gathered as follows: For the variegated group, d_p to v , c_1 and f_d ; D to c_1 ; w_2 to v , c_1 , f_d and c_u ; d_o to v , c_1 and c_u ; e to v and c_1 . For the cordate group, d_p to c_o and f_e ; w_2 to c_o , f_e , s_c , p_c and c_p ; d_o to c_o , f_e , s_c and c_p ; e to c_p . For the yellow group, d_p to y ; D to y and d_y ; d_o to y ; e to y . For the acuminate group, D to m_o ; w_2 to a_c and m_o ; d_o to a_c and m_o . For the contracted group, d_p to i_o , c_t , M_{r1} , i and d_k ; D to i ; w_2 to c_t , M_{r1} , i , d_k and R_y ; d_o to c_t (c_t^*), M_{r1} and d_k ; e to i and d_k . For the speckled group, d_p to s_p ; w_2 to s_p and w_1 ; d_o to w_1 ; e to w_1 . For the delicate group, d_p to d_1 . For the pear group, w_2 to p ; e to p .

RETRACTED LINKAGE GROUP

Retracted (*r*) is transmitted independently with respect to the following genes: v , c_1 , B_1 and f_d of the variegated group; c_o of the cordate group; y and s_p-r of the yellow group; m_o of the acuminate group; c_t (c_t^*), M_{r1} , t_w , d_k and R_y of the contracted group; s_p and w_1 of the speckled group; d_1 of the delicate group; p of the pear group; d_p , w_2 and d_o of the duplicated group. These data show retracted not to be included in the linkage groups above mentioned, but in a different group.

Foliate (f_o), a recessive modifier of terminal (t), is found to be linked very closely with retracted, as indicated by the data in table 24.

Therefore the retracted linkage group contains the two genes, retracted and foliate.

TABLE 24
F₂ from the cross of retracted (foliate) by terminal.

CROSS	+	<i>r</i>	<i>t</i>	<i>f_o</i>	<i>r t</i>	<i>r f_o</i>	TOTAL
461×415	86	34	28	0	0	13	161

MISCELLANEOUS

Besides the ten linkage groups above represented, a gene is found which seems to be independent to them, and may be included in another group. Some other genes have been proved to be independent of the genes of some linkage groups, but their relations to the other groups have not been studied as yet. As regards such genes the extent of the proof of independence by experiments is as follows: Maple or m^w (willow, allelomorph to m) to v , c_1 and B_1 of the variegated group; c_o , f_e , s_c and c_p (c_p^*) of the cordate group; y and d_y of the yellow group; a_c and m_a of the acuminate group; i_a , c_t , t_w , i , m_{r-r^*} and d_k of the contracted group; s_p and w_1 of the speckled group; d_l of the delicate group; p of the pear group; d_p , w_2 and d_a of the duplicated group; r of the retracted group. Polymorphic to v , c_1 and B_1 of the variegated group; c_o , s_c and c_p of the cordate group; y and d_y of the yellow group; a_c of the acuminate group; c_t of the contracted group; d_l of the delicate group; p of the pear group; w_2 and d_a of the duplicated group; r of the retracted group; and m of group yet undetermined. White-3 to v , c_1 and f_d of the variegated group; c_o , s_c and c_p of the cordate group; M_{r2} of the acuminate group; M_{r1} and d_k of the contracted group; w_1 of the speckled group; D , w_2 and d_a of the duplicated group; r of the retracted group; and m and M_{r-s} (Margined-suppressed). Buff to v of the variegated group; c_p^* of the cordate group; i of the contracted group; w_1 of the speckled group; p of the pear group; w_2 and e of the duplicated group; and w_3 . Crisscrossed to c_1 and f_d^* of the variegated group; c_o and c_p^* of the cordate group; c_t , i and t_w of the contracted group; d_l of the delicate group; and m^w . Deficient to c_1 of the variegated group; c_o and c_p of the cordate group; i_a , i and p_r of the contracted group; w_2 of the duplicated group. Terminal to v and c_1 of the variegated group; c_o of the cordate group; d_k of the contracted group; w_1 of the speckled group; w_2 and d_a of the duplicated group; r of the retracted group; and w_3 . Glabrous to v and c_1 of the variegated group; m_a of the acuminate group; c_t and

M_{r1} of the contracted group; d_o of the duplicated group; r of the retracted group. Wrinkled to d_y of the yellow group; m_o of the acuminate group; M_{r1} of the contracted group; and g (glabrous). Contorted to c_p of the cordate group; d_y of the yellow group; m_o of the acuminate group; c_t , i , M_{r1} and p_r of the contracted group; w_2 of the duplicated group; r of the retracted group; and m and p_y (polymorphic). Petaloid to v of the variegated group; c_o , f_e , s_c and c_p of the cordate group; y of the yellow group; d_k of the contracted group; w_2 and d_p of the duplicated group; and m . Tinged to c_1 of the variegated group; D and w_2 of the duplicated group. Variegated-reduced to v of the variegated group; s_c of the cordate group; y^i and l_t of the yellow group; M_{r1} of the contracted group; d_o of the duplicated group. Side-reduced to y of the yellow group; c_t of the contracted group; r of the retracted group. Lined to c_1 of the variegated group; d_o of the duplicated group; and f_i (flecked).

CONCLUSION

Almost simultaneously, but independently, three authors fixed the chromosome number of *Pharbitis Nil* (YASUI 1928, NAGAO 1928, KANÔ 1929). The haploid number was found to be 15. According to the writer's investigation, ten linkage groups have been established. There may be still five other linkage groups not yet represented by discovered cases of linkage. Up to the present time, over one hundred genes have been detected in this plant (IMAI in press). The genes subjected to the linkage analysis are about 70, of which 50 loci are found to be included in the ten linkage groups with the following distributions:

- (1) Variegated linkage group v , c_1 , B_1 , f_3 , b_r , e_o , $f_d(f_d^s)$, c_u .
- (2) Cordate linkage group c_o , f_e , s_c , p_e , p_1 , $c_p(c_p^r)$.
- (3) Yellow linkage group $y(y^i)$, d_y , l_t , d_e , s_p-r .
- (4) Acuminate linkage group a_o , M_{r2} , m_o .
- (5) Contracted linkage group R_y , c_r , i_o , s_h , c_t , M_{r1} , t_w , i , M_{r-r}
(m_r-r^s), d_k , p_r .
- (6) Speckled linkage group s_p , w_1 , M_{r-f} .
- (7) Delicate linkage group d_1 , c_2 .
- (8) Pear linkage group p , f_1 , f_2 , B_2 .
- (9) Duplicated linkage group d_p , s_t , D , w_2 , d_o , e .
- (10) Retracted linkage group r , f_o .

The interrelations between these groups have been found to be independent, so far as the writer's investigation is concerned. The proofs seem to be nearly sufficient to regard them as being different linkage

groups related to the different chromosomes, when an independent relation between the speckled and delicate groups is proved.

SUMMARY

1. Ten linkage groups have been established in *Pharbitis Nil*, including 50 loci. So far as the writer's experiments are concerned, the relations between these groups have been found to be independent.

2. The variegated linkage group is composed of eight genes, variegated (*v*), crumpled-1 (*c*₁), Blown-1 (*B*₁), fasciated-3 (*f*₃), brown (*b*_r), even (*e*_v), faded (*f*_d) and couple (*c*_u). The frequency of recombination is 17.7 for *v* and *c*₁, 29.3 for *v* and *B*₁, roughly 20–25 for *v* and *f*₃, and about 31.0 for *v* and *f*_d. The *b*_r locus seems to be situated not far from those of *v* and *c*₁, and *e*_v also from that of *v*. Couple is linked with *v*; the recombination frequency is about 37.7 percent; and its location on the chromosome may be *c*₁—*v*—*c*_u, or *vice versa*.

3. The cordate linkage group was noted as containing three genes, cordate (*c*_o), feathered (*f*_e) and semi-contracted (*s*_c). The linear arrangement of these genes in the chromosome is probably *c*_o—*f*_e—*s*_c, with a distance of 1.2 between *c*_o and *f*_e, and 17.7 between *f*_e and *s*_c. Precocious (*p*_c) is found to be linked with *c*_o, the recombination percent being about 24.6. The other two genes, palmate (*p*_i) and crêpe (*c*_p), are linked with each other with 34.6 percent of recombination, and are also linked with *p*_c. The recombination frequency is about 31.3 percent for *p*_c and *p*_i, and about 38.8 percent for *p*_c and *c*_p. Crêpe is located farther than *p*_c from *c*_o.

4. The yellow linkage group contains five genes, yellow (*y*), dusky (*d*_y), light (*l*_t), deformed (*d*_e) and speckled-reduced (*s*_{p-r}). The frequency of recombination for *y* and *d*_y is 1.0 percent, showing a very short distance between the two loci. Light is linked rather closely with *y* as well as with *d*_y. Speckled-reduced is located about 28.5 units from *y*, and *d*_e is about 15 units from the same.

5. The acuminate linkage group was known to include three genes, acuminate (*a*_c), Margined-2 (*M*_{r2}) and magenta (*m*_g). The recombination percent is about 0.5 for *a*_c and *M*_{r2}, and 21.2 for *a*_c and *m*_g. No new genes have been detected for this group.

6. The contracted linkage group includes eleven genes, interaxil-green (*i*_g), contracted (*c*_t), Margined-1 (*M*_{r1}); tube-white (*t*_w), intense (*i*), Margined-reduced (*M*_{r-r}), shrubby (*s*_h), Rayed (*R*_y), cream (*c*_r), duskish (*d*_k) and purple (*p*_r). Experimental data giving rough material make possible the drawing of a preliminary chromosome map of the following

relations: $R_v(0)$, $c_r(\pm 1.2)$, $i_g(10.3)$, $s_k(10.3 \pm 3.1)$, $c_t(15.8)$, $M_{r1}(16.8)$, $t_w(23.9)$, $i(48.5)$, $M_{r-r}(48.5 \pm 3.0)$. The loci of the two genes, duskish and purple, seem to be in the right part of the chromosome.

7. The speckled linkage group was noted as containing three genes, speckled (s_p), white-1 (w_1), and Margined-fluctuated (M_{r-f}); the recombination percent is about 0.8 for s_p and w_1 , and roughly 20 for w_1 and M_{r-f} . No genes have been analyzed to add new members for this group.

8. Only two genes, delicate (d_l) and crumpled-2 (c_2), have been found to compose the delicate linkage group. The recombination frequency for d_l and c_2 is roughly 5 percent.

9. The pear linkage group was found to include four genes, pear (p), fasciated-1 (f_1), fasciated-2 (f_2) and Blown-2 (B_2). The recombination percent is roughly 20–25 for f_1 and f_2 , about 2.5 for p and f_1 , and 23.5 for p and B_2 . No new genes have been determined for this group.

10. The duplicated linkage group is composed of six members, duplicated (d_p), striped (s_t), Dilute (D), white-2 (w_2), dragonfly (d_g) and extended (e). The recombination percentage is 13.7 for d_p and s_t , 25.6 for d_p and D , 10.1 for s_t and D , less than 1.4 for D and w_2 , 23.3 for w_2 and d_g , and 38.3 for d_g and e . Their order on the chromosome may be $d_p-s_t-D \pm w_2-d_g$, with an interval of 13.7 between d_p and s_t , 10.1 between s_t and D , and 23.3 between w_2 and d_g . Extended is located at a distance of 38.3 units on either the left or the right side of d_g .

11. The retracted linkage group is composed of two genes, retracted (r) and foliate (f_o), the recombination frequency being low.

12. Some other genes, which are independent of those included in the ten linkage groups, are presented.

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